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Rhythmic swaying induced by sound in chimpanzees (*Pan troglodytes*)

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Music and dance are universal across human culture and have an ancient history. One characteristic of music is its strong influence on movement. For example, an auditory beat induces rhythmic movement with positive emotions in humans from early developmental stages. In this study, we investigated if sound induced spontaneous rhythmic movement in chimpanzees. Three experiments showed that: 1) an auditory beat induced rhythmic swaying and other rhythmic movements, with larger responses from male chimpanzees than female chimpanzees; 2) random beat as well as regular beat induced rhythmic swaying and beat tempo affected movement periodicity in a chimpanzee in a bipedal posture; and 3) a chimpanzee showed close proximity to the sound source while hearing auditory stimuli. The finding that male chimpanzees showed a larger response to sound than female chimpanzees was consistent with previous literature about "rain dances" in the wild, where male chimpanzees engage in rhythmic displays when hearing the sound of rain starting. The fact that rhythmic swaying was induced regardless of beat regularity may be a critical difference from humans, and a further study should reveal the physiological properties of sound that induce rhythmic movements in chimpanzees. These results suggest some biological foundation for dancing existed in the common ancestor of humans and chimpanzees ∼6 million years ago. As such, this study supports the evolutionary origins of musicality.

rhythmic movement | chimpanzees | evolution | music | dance

Music-Induced Movement in Humans

Music and dance are universal across human culture and have an ancient history (1–3). Several hypotheses have been suggested to explain the evolutionary origins of music and dance, such as courtship displays (4), group cohesion (5–7), and coalition signaling (8). However, much remains unknown. Comparing humans' "musicality," defined as a human biological predisposition to process music (9), with that of nonhuman animals may be an excellent tool to understand how this unique communication developed in the course of human evolution.

From an early stage of development, human infants spontaneously engage in movement to music (10, 11). Later, this movement becomes more accurately synchronized with the pulse of music (12). This response is facilitated more often in social contexts than nonsocial contexts (13), suggesting humans' advanced rhythmic ability may have been selected for coordination among multiple individuals (14).

Neurobiological studies have shown that this advanced rhythmic ability depends on close connections between auditory and motor areas in the human brain (for overviews, see refs. 15 and 16). Motor areas in the brain are recruited even when humans listen passively to beat-based rhythms, suggesting the motor system plays an important role in processing such rhythms. For example, a study using functional magnetic resonance imaging instructed participants not to move when perceiving the beat (17). Despite the lack of movement, that study found increased levels of activity in the putamen (basal ganglia) and supplementary motor area when listening to beat-based versus nonbeat-based rhythms (17).

Although previous studies have largely focused on finger tapping to reveal rhythmic ability in humans, music induces a variety of body movements. Research suggests that when humans dance to music, the whole body and body parts are entrained differently at each metrical level (18–20). For example, a recent study using an optical motion capture technique found that certain beat- and rhythm-related musical characteristics (e.g., pulse clarity and spectral flux in low and high frequency components) influenced participants' movements, such as increased speed and more overall movement with high pulse clarity (18). These results suggest that music strongly induces spontaneous rhythmic movement in humans, and various features of music influence movement at different levels.

Spontaneous Response to Auditory Beat in Nonhuman Animals

Recently, it has been shown that some nonhuman animals also have an ability to entrain their body movement to an auditory rhythmic beat, including parrots (21, 22), a sea lion (23, 24), a bonobos (25), and chimpanzees (26, 27). However, most previous studies focused on the relationship between movement timing and auditory rhythms; relatively little attention has been paid to how sound induces movement (see ref. 28 and *Discussion*).

Does an Auditory Beat Induce Rhythmic Movement in Chimpanzees

Chimpanzees are considered an ideal candidate to reveal the evolutionary origins of human music ability because they are 1 of the closest living relatives to humans. Although they have limited ability to control their vocal cords (29), chimpanzees show various kinds of activities that could be considered prerequisites for

Significance

In humans, listening to music induces rhythmic movement, suggesting a close connection between the auditory and motor areas in the brain. Sound also induces rhythmic swaying in chimpanzees. Male chimpanzees are more responsive to sound than female chimpanzees, consistent with previous research on acoustic communication in their patriarchal societies. We also found an effect of beat tempo on movement periodicity and tendency to seek the sound. These results suggest that prerequisites for music and dance are deeply rooted and existed in the common ancestor shared by humans and chimpanzees, approximately 6 million years ago.

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The authors declare no competing interest.

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human music, including drumming on tree buttresses (30, 31), chorusing between group members (32), and playfully making sounds with objects (33).

Researchers have reported that chimpanzees perform "rain dances" and "waterfall dances" in the wild (34–37). At the start of heavy rain, adult male chimpanzees show rhythmic swaying that contrasts with normal charging displays in the lack of intimidation of other chimpanzees. These displays are considered some kind of collective response to the sound and fury of nature and have been linked to human rituals in response to natural forces that are sensorially overwhelming (38). However, despite its existence being known for more than 40 years (39), the rain dance has not been analyzed in detail.

We experimentally investigated how sound stimuli induced rhythmic body movement in chimpanzees to clarify the nature of their response to sound. Specifically, we examined: 1) how an auditory beat at different tempi induced rhythmic body movement in chimpanzees (Experiment 1); 2) if beat tempo affected movement periodicity (Experiment 2); and 3) if chimpanzees showed any tendency for spatial proximity to the auditory source while hearing the beat (Experiment 3).

Results

Experiment 1: An Auditory Beat Induced More Rhythmic Movement in Male than Female Chimpanzees. We used a typical 2-measure rock drum accompaniment pattern that was previously used in studies with infants and macaque monkeys (40, 41). This comprised piano sounds C1, C2, and C3 (Fig. 1*A*) spanning 8 equally spaced (isochronous) positions. Although a percussion instrument is usually used for making beat sounds (e.g., refs. 40–42), we used a piano sound that we had used in previous studies (26, 27) because in an earlier pilot study, our chimpanzees showed signs of distress in response to a novel sound timbre. We prepared the sound stimuli at 6 different tempi (i.e., 188 bpm, 167 bpm, 150 bpm, 94 bpm, 83 bpm, and 75 bpm), including extremely fast and slow tempo stimuli. This was because no previous study concerning the effect of tempo on rhythmic movement in primates was available, meaning it was difficult to estimate the optimal tempo range. The chimpanzees did not receive rewards for matching their movement to a beat before or during this study.

We conducted a playback experiment in the chimpanzee experimental booth (Fig. 1*B*). One session comprised 6 trials. Each sound stimulus was played for 2 min (120 s) in each trial. The order of the 6 stimuli was randomized for each session. One session was conducted per day, with a total of 6 sessions. The intertrial interval was ∼20 s. To avoid carryover effects, we confirmed the chimpanzees did not make any rhythmic movement for at least 10 s before beginning a trial. The chimpanzees' behaviors during the experiment were video recorded at a sampling rate of 60 frames per sec (fps) and analyzed later.

Observed rhythmic movements. Rhythmic movement was defined as repetitive movement of the whole body or body parts more than 3 times, which is behavior the chimpanzees did not usually show in the experimental booth. Observed rhythmic movements are summarized in Table 1 (see Movies S1–S4 for examples). The chimpanzees mostly swayed their whole body, but rhythmic movements of body parts such as hand clapping or foot tapping were also observed.

Effects of sex and tempo on rhythmic swaying while playing sound stimuli. To investigate the effect of tempo and sex difference on rhythmic swaying, we conducted linear mixed models (LMM) with rate of swaying duration as a dependent variable. We included tempo and sex as fixed variables and participant ID as a random effect. We found a significant effect of sex (parameter estimate [Est] = −25.76; df = 5.0; $t = -3.024$; $P = 0.029$) (Fig. 1*C*). This tendency suggested that male chimpanzees were more responsive to the sound stimuli than female chimpanzees.

Effect of sex on vocalization. Rhythmic swaying was sometimes accompanied by vocalization (Movie S5). We analyzed the number of trials during which the chimpanzees vocalized based on the video recordings, which allowed us to detect the occurrence of vocalizations, although it was difficult to specify onset and end. A LMM was performed using the number of trials in which vocalization was made as the dependent variable. The independent variables were sex and tempo, and the random effect was participant ID. We found a significant effect of sex (Est = −2.94; df = 15.30; $t = -3.03$; $P = 0.0083$), indicating that male chimpanzees vocalized in more trials than female chimpanzees (Fig. 1*D*).

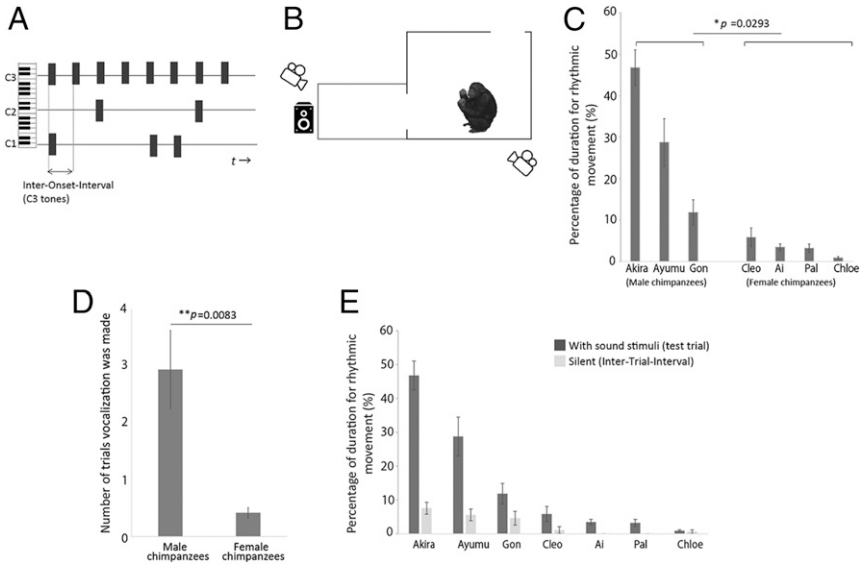

Fig. 1. (*A*) Schematic drawing of the sound stimuli. Each sound was made up of an acoustic piano sound. Sound stimulus was made by manipulating interonset interval of C3 tones. (*B*) Schematic drawing of the experimental setting. (*C*) Percentage of duration for rhythmic movement observed while playing auditory stimuli in Experiment 1. (*D*) Average number of trials in which vocalization was recorded in Experiment 1. (*E*) Percentage of duration for rhythmic movement in test trials and intertrial intervals.

Table 1. Percentage of rhythmic movement observed

	Whole body movement			Partial body movement			
	Bipedal sway	Quadrupedal sway	Hanging sway	Hand clapping	Knocking/banging	Foot tapping	Combination of whole body and partial body
Akira (M)	75.28	22.08	0.31	0	1.07	0	0.81
Ayumu (M)	62.99	9.7	25.37	0	0.62	0	1.32
Gon (M)	6.84	52.11	0	8.07	32.32	0	0.66
Cleo (F)	64.26	28.14	0	5.85	1.74	0	0
Ai (F)	46.89	0	3.5	0	0	49.62	0
Pal (F)	1.6	8.13	11.23	55.83	12.15	0	0
Chloe (F)	0	0	100	0	0	0	0

Bipedal sway, swaying in an upright, 2-legged stance; Quadrupedal sway, swaying while standing on all fours; Hanging sway, swaying when hanging from ceiling bars; Hand clapping, clapping the hands; Knocking/banging, knocking or banging a panel with the hands; Foot tapping, tapping the foot. F, female; M, male.

Rhythmic movement while playing sound stimuli versus silence. We compared the percentage of duration of rhythmic engagement between the test trials with auditory stimuli and the intertrial interval (silence) to confirm that these behaviors were driven by the auditory stimuli. We performed a LMM using the percentage of duration for rhythmic movement as the dependent variable, the presence of sound (playing sound stimuli [test trial] vs. silence [intertest-interval]) as the independent variable, and participant ID as the random effect. The presence of sound had a significant effect (test trial vs. intertrial interval: Est = −11.606; df = 76.0; $t = -5.656$; $P < 0.001$) (Fig. 1*E*). This confirmed that the auditory stimuli induced rhythmic engagement in the chimpanzees.

This experiment showed that chimpanzees spontaneously engaged with an auditory beat. The auditory stimulus induced more rhythmic movement and vocalization in male than female chimpanzees. This suggests that male chimpanzees may be more sensitive and responsive to auditory stimuli and was consistent with other literature regarding wild chimpanzees. For example, studies reported that acoustic communication occurs more frequently in male chimpanzees than female chimpanzees, including drumming (30, 31) and chorusing between members (32). Therefore, superior sensitivity to sound in males compared with females may reflect chimpanzees' patriarchal society, where males frequently use acoustic communication to confirm their social relationships and protect their territory and members.

In Experiment 2, we further investigated if beat tempo affected movement periodicity, focusing on 1 39-year-old male chimpanzee (Akira) who responded to the auditory stimuli particularly strongly in Experiment 1.

Experiment 2: Stimulus Tempo Affected Movement Periodicity in a Chimpanzee. In this experiment, we investigated the effect of the type of rhythm on movement using the same procedure as in Experiment 1. Specifically, we tested if a random rhythm induced rhythmic swaying and also examined the effect of beat tempo on movement periodicity. We focused on the male chimpanzee (Akira) who showed most rhythmic movement in Experiment 1 (more than 50% of the time the sound was played). We assumed that Akira would be the only participant from whom we could collect sufficient quantitative data to compare different conditions.

The procedure was exactly the same as in Experiment 1, but we used 4 sound stimuli (i.e., 150 bpm, 107 bpm, 83 bpm, and random) (*SI Appendix*, Fig. S1 and Audio S3). We included the random condition to determine if this also induced rhythmic movement in the chimpanzee. One session comprised 4 trials covering all 4 conditions. Only 1 session was conducted per day. All combinations of the order of sounds were tested across 24 sessions over 24 d. Each sound stimulus lasted for 2 min, and the intertrial interval was ∼20 s. The chimpanzee's behaviors during the experiment were video recorded at a sampling rate of 120 fps and analyzed later.

We analyzed the duration of the chimpanzee's rhythmic movement. A 1-way repeated-measures analysis of variance (ANOVA) (tempo × order) revealed no difference in duration of induced rhythmic movements across the sound stimuli ($F[3, 69] = 1.329$, $P = 0.273$) (*SI Appendix*, Fig. S2). Therefore, the random rhythm induced rhythmic movements as much the beat-based sounds.

Akira showed 2 types of swaying movements (i.e., swaying in quadrupedal and bipedal postures). He swayed horizontally in a quadrupedal posture and vertically in a bipedal posture. Therefore, we analyzed the effect of beat tempo on movement periodicity separately for each posture. We transferred video images of swaying segments to static images. Then, head movement was tracked by putting markers on a salient part (e.g., nose, forehead, or ear) using MTrack J in ImageJ (Fig. 2 *A* and *C*). Using the tracking data (x and y coordinates), the peak periodicity of rhythmic movement was analyzed with the Mocap Toolbox in Matlab (see *SI Appendix* for the analysis).

Because of the movement direction in each posture, we analyzed correlations between peak periodicity of vertical movement and beat tempo in the bipedal posture, and between peak periodicity of horizontal movement and beat tempo in the quadrupedal posture (Fig. 2 *B* and *D* and Movies S2 and S3). The tempi of auditory stimuli were obtained by 2 experimenters independently tapping along with the stimuli. In bipedal sway movements, there was a significant positive correlation between vertical movement periodicity and beat tempo ($r = 0.612$, $P = 0.005$). However, there was no significant correlation in horizontal periodicity in the quadrupedal sway movements.

Experiment 3: Tendency for Proximity to the Sound Source. Spatial proximity has been used as a possible preference index in numerous studies. A recent study showed that chimpanzees stayed close to sound source more when hearing African and Indian music compared with silence (43); however, another study found no such persistent tendency (44). Therefore, we conducted an experiment focusing on Akira's spatial proximity using an ABA design. In addition to Experiments 1 and 2, we added 2 other playback experiments. In 1 of these additional experiments, no sound was played and in the other, sound stimuli were played again. We tested whether the chimpanzee's spatial proximity to the sound source changed depending upon the presence of auditory stimuli. We analyzed the percentage of time Akira spent in the area near the auditory source in each condition (Fig. 3 *A* and *B*).

A 1-way repeated-measures ANOVA revealed that Akira stayed significantly longer in the auditory source area when he heard the auditory stimuli than when no sound was played ($F[2, 47] = 9.525$, $P < 0.0001$; post hoc tests with Bonferroni correction: Experiments 1 and 2 vs. Experiment 3 [silence], $P < 0.001$; Experiment 3

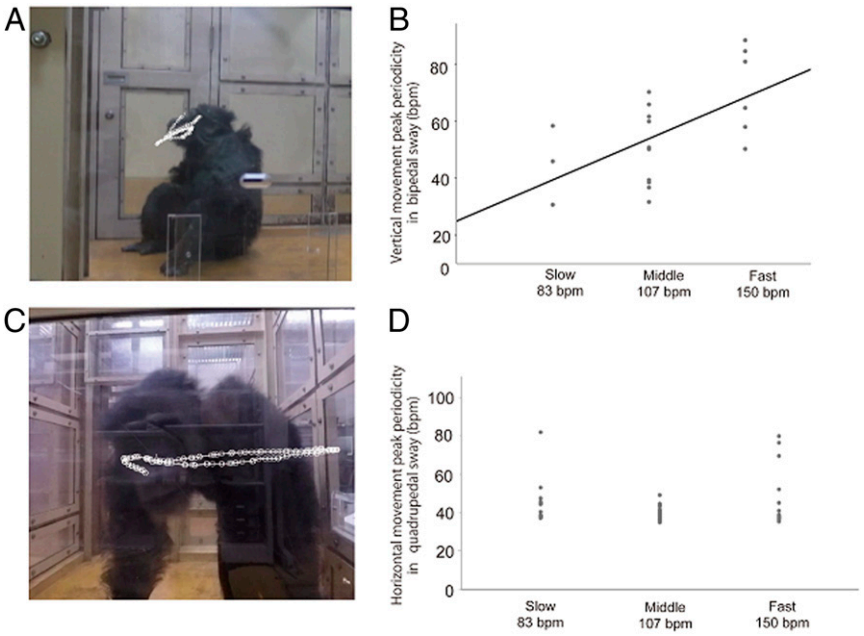

Fig. 2. (*A*) Picture of Akira in a bipedal posture with tracking markers on his nose. (*B*) Correlation between movement periodicity and beat tempo in the bipedal posture. (*C*) Picture of Akira in a quadrupedal posture with tracking markers on his nose. (*D*) Correlation between movement periodicity and beat tempo in the quadrupedal posture.

[silence] vs. Experiment 3 [sound played], $P = 0.029$). As shown in Fig. 3*B*, Akira did not stay in the auditory source area when he detected that no sound was played. This suggested that the sound source area was not simply a preferred location for him. Akira sought auditory stimulation, so approached the source area and stayed longer when the auditory stimuli were played.

Discussion

We investigated if sound induced rhythmic movement in chimpanzees, and if so, to what extent the beat affected movement periodicity and spatial proximity to the sound source. In Experiment 1, we showed that chimpanzees were induced to move rhythmically by auditory stimuli. Furthermore, we found that male chimpanzees showed a larger response than female chimpanzees in terms of duration of rhythmic movement and frequency of vocalization. These findings suggested that male chimpanzees are more sensitive than females to rhythmic auditory stimuli, consistent with literature about rain and waterfall dances in the wild. Other reports that auditory communication, such as pant-hoots or buttress drumming (e.g., refs. 30–32), are mostly performed by male chimpanzees also support a sex difference in sound sensitivity. Given that humans do not have such a sex difference in musical ability, higher sensitivity to sound in male chimpanzees may have been acquired after chimpanzees diverged from the common ancestor shared with humans. This may also be associated with their patriarchal society, where male chimpanzees often collaborate to protect their territory and group members.

Overall, the rhythmic movement observed in this study was whole body movement such as rocking or swaying, with accompanying head movements. A study in humans suggested that such movements are related to perceiving rhythm by generating a vestibular signal that underlies the sense of meter (45). Another study showed that vestibular stimulation also occurs when listening to loud (90 dB) dance music, possibly contributing to the pleasurable experiences associated with dancing to such music (46). Although the sound intensity used in this study was lower than 90 dB (i.e., 75 dB) and is unlikely to have caused direct activation of the vestibular system, it may be possible that the vestibular sensory-motor network underlies rhythmic swaying to sound in chimpanzees (47).

In animal welfare research, rhythmic movement such as swaying or rocking is sometimes described as "stereotyped behavior." For example, isolation-reared chimpanzees showed rhythmic swaying and rocking when they heard white noise more than when no sound was played (48). However, all of our chimpanzees were group-raised and none showed stereotyped behaviors in daily life. Furthermore, they participate in experiments on a voluntary basis. Before starting an experiment, researchers come to the chimpanzees' enclosure and call their

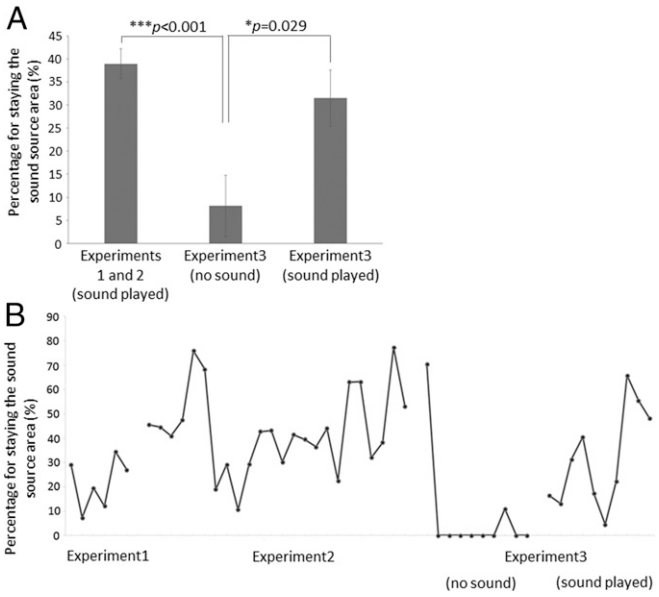

Fig. 3. (*A*) Average percentage of duration near the sound source area in Experiments 1–3. (*B*) Time series of percentage of duration near the sound source area in each session of Experiments 1–4.

name. The researchers can guide the chimpanzee only when the latter voluntarily enters a tunnel connected to an experimental booth. Considering this and together with Akira's proximity to the sound source, it is unlikely that the sound stimulus was aversive, and the chimpanzees were distressed by the sound. Rather, the sound gave an optimal stimulus so the chimpanzees voluntarily came to the place where they could hear the sound.

Nevertheless, some stereotyped behaviors may be reinforced as coping mechanisms (49). Just as rocking soothes human babies (50), repetitive rhythmic movement may have some calming effect (51). Given that the definition of stereotyped behavior is "repetitive, invariant behavior patterns with no obvious goal or function" (52), the observed behaviors in this study could be classified as stereotypies. By comparing the effect of sound on rhythmic swaying and other stereotyped behaviors (53), possible underlying mechanisms of this response (e.g., vestibular system) may be revealed in further studies.

In Experiments 2 and 3, we focused on 1 male chimpanzee (Akira) who showed the largest response among our participants to rhythmic auditory stimuli. In Experiment 2, we tested the effect of sound stimuli (including a random beat) on rhythmic movement duration and periodicity. With the same procedure as in Experiment 1, we found no significant difference in movement duration across the sound stimuli (i.e., 150 bpm, 107 bpm, 83 bpm, and random). Therefore, an isochronous auditory beat was not a necessary condition to induce rhythmic movement in the chimpanzee. Considering this and the fact that tempo affected Akira's rhythmic swaying, it was possible that Akira responded to sound event density rather than rhythm per se. This may indicate a critical difference from humans, as human infants' movements are already affected by beat regularity and also by beat tempo (11), and such behaviors are robust in human adults (18–20). Specific sound factors related to inducing rhythmic movement in chimpanzees need to be clarified in further studies.

In Experiment 2, we also analyzed the effect of beat tempo on movement periodicity. Akira showed 2 types of movement (i.e., swaying in bipedal and quadrupedal postures) with different directions; that is, vertical movement in the bipedal posture and horizontal movement in the quadrupedal posture (Fig. 2 *A* and *C*). Therefore, we analyzed these movements separately. We found a significant correlation between movement periodicity and beat tempo in the bipedal posture only. This may be attributable to differences in freedom of movement in each posture. For example, when bipedal, 2 legs are fixed on the floor and the upper body can move flexibly, whereas both hands and legs are fixed in a quadrupedal posture, so movements are less flexible.

In Experiment 3, we tested Akira's spatial proximity to the sound source. If he had a positive response to the sound or perceived the sound as an optimal stimulus, we expected him to stay close to the sound source area while hearing the stimuli. Conversely, he was expected to avoid the sound source area if he had a negative response to the sound. The results showed that Akira stayed around the sound source area longer when there was auditory stimulation than when there was no sound. Conceivably, he responded more positively to a stronger sound intensity, and therefore his spontaneous rhythmic movement might have been rewarding rather distracting. However, caution is required when interpreting this result as data were collected from only 1 chimpanzee; a general preference for an auditory beat at a species level remains to be confirmed. Nevertheless, Akira's clear tendency to seek the auditory source was consistent with a description of male chimpanzees approaching the site of a 10-m-high waterfall to perform rhythmic swaying (36).

Recently, it has been reported that music induced various kinds of rhythmic movement in a cockatoo called "Snowball" (28). Comparing Snowball's movement repertoire with that of the chimpanzees showed head bobbing was observed in both studies, whereas other movements such as the head following a semicircle trajectory were not observed in our chimpanzees. Therefore, there may be some biomechanical constraint in such music/sound-induced movement. Another interesting point was that the duration of rhythmic movement was much longer in chimpanzees than in Snowball. On average, Akira showed rhythmic swaying for about 43 s per bout (Experiment 2: mean duration 42.67 ± 30.09 s; $n = 144$) whereas Snowball's "dancing" lasted about 4 s on average per bout (mean duration 3.69 ± 2.72 s; $n = 141$). Although a clear relationship between acoustic events and movement was not observed in our chimpanzees or in Snowball, beat tempo (or acoustic event density) affected movement periodicity in the chimpanzees. It would be interesting to investigate species-based differences in music induced-rhythmic movement in more detail in further studies.

Primate Origins of Music and Dance. Concerning the evolutionary process of human musicality in primate lineage, the gradual audiomotor (GAE) hypothesis (41, 42, 54) claims that rhythmic entrainment (or beat-based timing) was gradually developed in primates, peaking in humans but present only with limited properties in other nonhuman primates. Conversely, another hypothesis ("vocal learning and rhythmic synchronization hypothesis") claims that advanced rhythmic ability, such as beat perception and synchronization (BPS), is a by-product of the complex vocal learning mechanisms that are shared by several bird and mammalian species including humans (16). A crucial difference between these hypotheses is that the GAE hypothesis suggests rhythmic entrainment evolved through a gradual chain of anatomical and functional changes in timing mechanisms, whereas the latter hypothesis considers evolution for vocal learning has an essential role in such advanced rhythmic ability. Given that spontaneous rhythmic engagement with sound in chimpanzees lacks accuracy and appeared regardless of the beat regularity, but has not been reported in monkeys, there appears to have been gradual development of a connection between auditory and motor areas in the brain in the course of human evolution. Previous studies support this concept by indicating that monkeys have difficulty synchronizing their movement to auditory rhythms (55) and are more sensitive to visual than auditory rhythms (56, 57), whereas chimpanzees spontaneously align their tapping to an auditory metronome or other's tapping sound (26, 27, 58). These findings suggest a strong connection between auditory and motor areas in the brain gradually evolved regardless of complex vocal learning ability. Based on that foundation, humans further developed more accurate rhythmic ability (e.g., BPS), perhaps in parallel with development of vocal learning ability (16).

In conclusion, our study showed that an auditory beat induced rhythmic movement in chimpanzees. The effect of sound in inducing rhythmic swaying is likely to have existed in the common ancestor shared by chimpanzees and humans ~6 million years ago. A sex difference in responsiveness to sound, with male chimpanzees being more sensitive and responsive to auditory stimuli than female chimpanzees, may have emerged after chimpanzees diverged from the common ancestor. The fact that both random and regular beats induced rhythmic movement suggests that regularity in sound rhythm is not essential for inducing rhythmic movement in chimpanzees. Future research should identify additional factors that influence rhythmic movement (e.g., using sound with a low frequency). However, beat tempo affected movement periodicity when a chimpanzee was in a bipedal posture, which suggests sound periodicity affects movement to some extent. We also found the chimpanzee approached the sound source while the sound stimulus was playing, suggesting a positive attraction to the sound. Further studies are needed to uncover more similarities and differences in responses to sound among chimpanzees, humans, and other species. Evidence suggests that some biological foundation for music and dance may be deeply rooted in the common ancestor shared by chimpanzees and humans. Comparing these phylogenetically

close species as well as more distant species will improve our understanding of the evolutionary role of music/ality and dance.

Materials and Methods

Ethics. The experimental protocol was approved by the Animal Welfare and Animal Care Committee of Kyoto University, Primate Research Institute (KUPRI) and the Animal Research Committee of Kyoto University (approval no. 2017-114). All procedures were in accordance with the Japanese Act on Welfare and Management of Animals. The care and use of the chimpanzees adhered to the 2010 version of the KUPRI Guide for the Care and Use of Laboratory Primates.

Procedure for Experiment 1. One male chimpanzee and 1 female chimpanzee participated along with their biological mothers because they did not want to be separated. Therefore, we kept the mother either in the corridor or a small room with a speaker connected to the main room (Fig. 1*A*). It was possible for the participant chimpanzees to see their mothers if they wished, but the overall distance between the participant chimpanzees and their mothers was more than 1 m. In addition, another experimenter engaged with and distracted the mother from the sound stimuli so she did not show any rhythmic responses or vocalization during the experiment. Therefore, even if the participant chimpanzee was paying attention to their mother, it was unlikely that the observed rhythmic movements and vocalizations in the participant chimpanzee was induced by observing their mother.

After an experimenter confirmed that the participant chimpanzee appeared calm and had not shown any rhythmic movement, a trial started and the sound stimulus was played for 2 min (120 s). After a trial finished, an intertrial interval was implemented (~20 s) so that the chimpanzee calmed down and showed no rhythmic movement. The experimenter again confirmed that the chimpanzee was calm state and had not shown any rhythmic movement for at least 10 s, and the next trial started.

The sound stimulus was made by manipulating onset-to-onset interval between successive sounds (i.e., onset-to-onset interval in C3: 80 ms = 188 bpm, 90 ms = 167 bpm, and 100 ms = 150 bpm with a sound duration of 50 ms, and 160 ms = 94 bpm, 180 ms = 83 bpm, and 200 ms = 75 bpm with a sound duration of 100 ms) (Fig. 1*A* and Audios S1 and S2).

To assess interobserver reliability in analyzing movement duration, 25% of the data were analyzed by another researcher who was blind to the purpose of this study. The Cohen's kappa coefficient for interobserver correlation was excellent (trials: $k = 0.827$; intertrial intervals: $k = 0.838$).

Procedure for Experiment 2. We prepared 4 sound stimuli manipulating the onset-to-onset interval between successive sounds (i.e., interval in C3: 100 ms = 150 bpm, 140 ms = 107 bpm, 180 ms = 83 bpm, and random). For the random stimuli, an auditory sequence was made with the interval randomly chosen (from 300 ms, 400 ms, 500 ms, 600 ms, 700 ms, and 800 ms) in each of tones C1, C2, and C3 for each pattern (*SI Appendix*, Fig. S1 and Audio S3). As in Experiment 1, 25% of the data were analyzed by another researcher who was blind to the purpose of this study. The interobserver correlation was excellent (test trials: $k = 0.815$).

Procedure for Experiment 3. After the experimenter confirmed Akira was behind the slide door, a trial started when the door was opened (*SI Appendix*, Fig. S3). A trial took 180 s (3 min). We tested only 1 trial in a day. In the silent condition, there was no sound during a trial. In the sound condition, we played the sound stimulus (interonset interval: 180 ms = 83 bpm) for 180 s. The experiment was recorded by 2 digital video cameras at a sampling rate of 60 fps. We analyzed Akira's location with Adobe Premier Pro CC 2017. We measured the percentage of the duration he stayed in the sound source area (*SI Appendix*, Fig. S3) for each trial. Sound intensity in the sound source area was 75 db, whereas it was 65 db in the center of the large experimental space.

All data discussed in the paper are available in *SI Dataset*.

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